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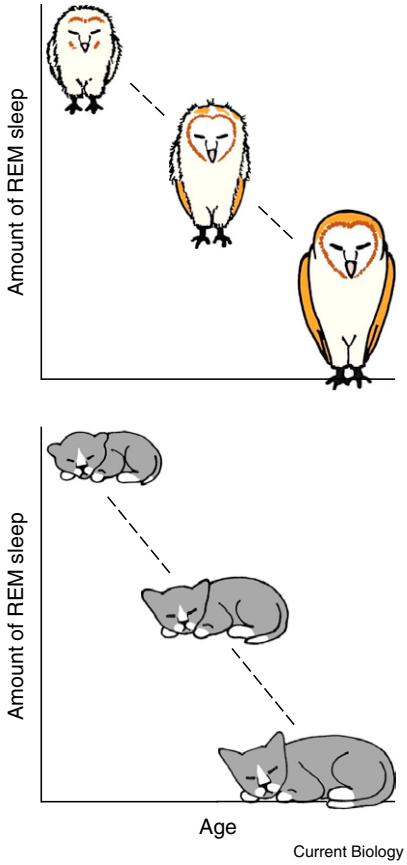

Figure 3. REM sleep ontogeny.
The amount of REM sleep decreases with age in young birds, as it does in young mammals (arbitrary units). Owlet and kitten drawings ©Ninon Ballerstädt.

activity during sleep. Interestingly, the pattern of firing observed is specific to the song heard, suggesting that the neuronal activity carries with it information about the song itself. However, the quality of the juvenile's song actually worsens after sleep, and improves only with practice the next day. Importantly, this effect is dependent upon sleep *per se*, as it is observed following daytime naps as well. The sleep-dependent deterioration of song quality seems detrimental at first glance; however, those birds whose song deteriorates the most during sleep ultimately reproduce the tutor's song best, indicating that this is an adaptive sleep process.

SWS and REM sleep must serve a purpose beyond developmental processes, however, as they persist into adulthood in both birds and mammals. The observation that SWS is more intense following brain use during wakefulness suggests that SWS serves a use-dependent neurophysiological role; however, the precise nature of this role is debated, with ideas ranging from restoring cellular resources depleted during wakefulness to weakening or strengthening synapses. The purpose of REM sleep in adults remains even more mysterious, as the suppression of REM sleep with anti-depressant drugs does not appear to impair performance in humans, and may even improve performance on motor memory tasks. Nevertheless, the abundance of REM sleep in neonates and its persistence throughout life suggests that REM sleep most likely serves processes prevalent in neonates that are needed less in adults. Ultimately, by determining the reason for the convergent evolution of SWS and REM sleep in birds and mammals, we may provide insight into the purpose of these states in ourselves.

Where can I find out more?

Abel, T., Havekes, R., Saletin, J.M., and Walker, M.P. (2013). Sleep, plasticity and memory from molecules to whole-brain networks. Curr. Biol. *23*, R774–R788.

Derégnaucourt, S., Mitra, P.P., Fehér, O., Pytte, C., and Tchernichovski, O. (2005). How sleep affects the developmental learning of bird song. Nature *433*, 710–716.

Lesku, J.A., Meyer, L.C., Fuller, A., Maloney, S.K., Dell'Omo, G., Vyssotski, A.L., and Rattenborg, N.C. (2011). Ostriches sleep like platypuses. PLoS ONE *6*, e23203.

Lesku, J.A., Vyssotski, A.L., Martinez-Gonzalez, D., Wilzeck, C., and Rattenborg, N.C. (2011). Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? Proc. R. Soc. B *278*, 2419–2428.

Lesku, J.A., Rattenborg, N.C., Valcu, M., Vyssotski, A.L., Kuhn, S., Kuemmeth, F., Heidrich, W., and Kempenaers, B. (2012). Adaptive sleep loss in polygynous pectoral sandpipers. Science *337*, 1654–1658.

Margoliash, D., and Schmidt, M.F. (2010). Sleep, off-line processing, and vocal learning. Brain Lang. *115*, 45–58.

Rattenborg, N.C., Lima, S.L., and Amlaner, C.J. (1999). Half-awake to the risk of predation. Nature *397*, 397–398.

Rattenborg, N.C., Martinez-Gonzalez, D., Roth, T.C., and Pravosudov, V.V. (2011). Hippocampal memory consolidation during sleep: a comparison of mammals and birds. Biol. Rev. *86*, 658–691.

Scriba, M.F., Ducrest A.-L., Henry, I., Vyssotski, A.L., Rattenborg, N.C., and Roulin, A. (2013). Linking melanism to brain development: expression of a melanism-related gene in barn owl feather follicles covaries with sleep ontogeny. Front. Zool. *10*, 42.

Shank, S.S., and Margoliash, D. (2009). Sleep and sensorimotor integration during early vocal learning in a songbird. Nature *458*, 73–77.

Siegel, J.M., Manger, P.R., Nienhuis, R., Fahringer, H.M., and Pettigrew, J.D. (1998). Monotremes and the evolution of rapid eye movement sleep. Philos. Trans. R. Soc. B *353*, 1147–1157.

Siegel, J.M. (2011). REM sleep: a biological and psychological paradox. Sleep Med. Rev. *15*, 139–142.

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Mosquitoes

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What are mosquitoes? Mosquitoes are delicate, long-legged two-winged flies (order Diptera, family Culicidae) that are easily recognized by their long proboscis and the scaly wings and legs (Figure 1). More than 3,500 species inhabit the temperate and tropical regions of the world. Females of many species suck blood — all males and many other females feed exclusively on nectar, fruit juices and plant exudates. Blood-sucking females require blood for egg development. Warm-blooded animals are a common source of blood, but many mosquito species also attack cold-blooded animals such as snakes, turtles, toads, frogs and other insects. Some species are active at night or twilight while others are active during the daytime.

How do mosquitoes reproduce? Females lay their eggs in water, where they develop into larvae, pupae and adults. Many species inhabit temporary or permanent bodies of ground water, but many others utilize container habitats such as tree holes, leaf axils and discarded tires. The larvae of most species feed on microorganisms and organic debris, but some are predators that feed largely on larvae of other mosquitoes. Mature larvae transform into pupae, which do not feed. Extensive anatomical changes take place within the pupa, and the adult emerges in two or three days.

The deadliest bite? Some blood-seeking mosquitoes attack only one or two host species, but most have no host preference and are opportunistic in their feeding behavior. Beyond simply annoying humans with their bites, fewer than 100 mosquito species are important because the females transmit ('vector') the viruses, filarial worms and protozoa that cause diseases such as yellow fever, lymphatic filariasis (elephantiasis), and malaria, respectively. The most important vectors have a marked tendency to feed on humans and inhabit domestic environments,

CrossMark

Figure 1. Mosquito diversity.
Left: the African species *Anopheles gambiae*, the world's most notorious malaria vector (photo by James Gathany). Middle: *Coquillettidia perturbans* female imbibing nectar (photo by Stephen A. Marshall). Right: the South American forest species *Sabethes cyaneus* — *Sabethes* species have a propensity for landing/biting on noses (photo by Anthony Guimarães).

such as the African malaria vector *Anopheles gambiae*, the dengue and yellow fever vector *Stegomyia aegypti* (formerly *Aedes aegypti*), and the filariasis vector *Culex quinquefasciatus*. This small subset of mosquito species is the indirect cause of more morbidity and mortality among humans than any other group of organisms.

How are vector mosquitoes identified and controlled? Mosquitoes are usually identified based on features of their external anatomy, such as the arrangement and form of setae (hairs) in larvae and the presence of setae and scales in adults. However, many of the major vectors of diseases such as malaria share distributions with several closely related, indistinguishable cousins of little or no medical importance. Such species are known collectively as 'cryptic' species complexes. The inability to distinguish vector and non-vector species is problematic for vector control, as it can result in needless expenditure of scarce resources in the impoverished tropical countries that suffer most from mosquito-borne disease. For the better-studied malaria vector species complexes, DNA-based methods have been developed that allow identification of individual species. Vector control measures aim to reduce or eliminate disease by killing larvae or adults and preventing blood-seeking females from making contact with people, *e.g.* by deployment of insecticide-impregnated bed nets.

Wouldn't the world be better off without mosquitoes? Mosquito larvae are food for fish and insect predators. Adult mosquitoes pollinate plants and are eaten by spiders, birds, bats, reptiles, and amphibians. Is it necessary to eradicate the messenger (mosquito) when it is really the message (pathogens and parasites) that is the enemy of public health? As a case in point, although malaria was eliminated in the United States and Europe during the first half of the 20th century, the mosquito vectors remain to this day.

I seem to get attacked by mosquitoes more than others, why is that? Conventional wisdom holds that mosquitoes attack some people more than others. Although this perception may be exaggerated, scientific evidence indicates that each person emanates a distinctive odor consisting of components of the breath, glandular secretions from the skin, and bacteria on the skin that a female mosquito can detect. Other factors, including health, pregnancy, and diet also seem to play a role (*e.g.*, beer consumption reportedly increases attractiveness to malaria vectors in West Africa).

What's the most unusual thing about mosquitoes? There are many! The genitalia of newly emerged adult males rotate 180° before mating; *Ochlerotatus irritans* in Africa has been observed feeding on fish, such as mud skippers, that partially lie out of the water; mosquitoes of the genus *Malaya* in Africa and Asia provoke ants to regurgitate and then suck up the fluid; the larvae of several genera use a modified breathing tube to pierce the stems and roots of aquatic plants to obtain oxygen; females of *Sabethes cyaneus* shoot their eggs through small openings into plant cavities while hovering; and the males of *Opifex fuscus* in New Zealand precociously couple with females before they have fully emerged from their pupal skin.

Is climate change going to benefit mosquitoes? Contrary to an often mentioned general concern, global warming is not a dominant factor in the spread of malaria and other mosquito-borne diseases, which, in addition to temperature, is affected by factors that include the vector species and their behavior, rainfall, agriculture, drug and insecticide resistance, public health services, cultural practices, and civil strife. Ecological and societal changes are the principal determinants.

Where can I find out more?

Clements, A.N. (1992, 1999, 2010). The Biology of Mosquitoes, Volumes 1–3 (New York: CABI Publishing).

Gillett, J.D. (1972). The Mosquito: Its Life, Activities, and Impact on Human Affairs (Garden City, New York: Doubleday & Company, Inc.).

Harbach, R.E. (2013). Mosquito Taxonomic Inventory, http://mosquito-taxonomic-inventory.info/, accessed on 26 August 2013.

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